BETWEEN THE TIDES ON THE KAIKOURA PENINSULA

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ABSTRACT

Thirteen intertidal areas around the Kaikoura Peninsula were surveyed using transects. Quantitative samples were taken using quadrats at 200 mm height intervals down the shore from the high water down to the extreme low water mark. All shores had a diverse fauna and flora with an average number of 58 species per transect. The fauna was dominated by herbivorous gastropods including several species with a typically northern distribution. Also included were southern species of algae such as *Durvillaea antarctica* and *Macrocystis pyrifera*. Translation of the transect data according to tidal height revealed a characteristic sequence of species down the shore. The number of species present and their vertical distribution was not directly related to the degree of exposure. Areas consisting of irregular limestone topography had similar numbers of species to the mudstone platforms. Species number was directly related to heterogeneity of the area, representing the diversity of available microhabitats present at upper, mid and lower-tidal levels.

Dissimilarity coefficients (Canberra Metric) were computed for species and sites on four transects containing rocky substratum at all shore levels. While for transect 1, the classification produced three species groupings, apparently without any biological significance, the combined results from two other transects (T6 and T9) identified four distinct groups. These corresponded to high shore and low shore species groups and two mid shore groups divided into the more mobile grazers and the sessile invertebrates and algae. Classification of the combined sites from T1, T6, T9 and T13, resulted in 5 groups separated mainly according to height above low water and in some instances distance along the transect. There was considerable within- and between-site variation and PCOORD analyses indicated considerable overlap between sites. The species responsible for the variation resulting in the classification were *Littorina cincta*, *L. unifasciata*, *Cellana denticulata* and *Chamaesipho columna*. Species and site classifications using dissimilarity indices therefore identified patterns which were not obvious from the original transect information. It also identified those species which appear to be important in describing the pattern and on which future work aimed at understanding factors responsible for the distribution, should be directed.

KEYWORDS: New Zealand intertidal zonation patterns, community analyses, dissimilarity coefficients, rocky shore ecology.

INTRODUCTION

During the late sixties, marine biologists all over the world, including New Zealand, were describing intertidal habitats in the search for universal patterns of zonation (Lewis, 1964; Morton and Miller, 1968; Stephenson and Stephenson, 1972). Organisms were thought to be grouped into characteristic bands at particular shore levels with only the species changing between geographical locations. More recently, it has been shown that on uniformly sloping shores with a gentle gradient, organisms are not necessarily aggregated according to tidal height (Underwood 1978), and that critical limits (Colman, 1933) resulting from tidal emersion and submersion do not occur on these shores. Furthermore, an increasing number of field experimentation studies have shown that biological rather than physical factors can determine both the upper and lower tidal limits of intertidal molluscs (see review by Underwood, 1979).

In New Zealand there has been little quantitative data available for intertidal communities. Detailed descriptions of shores are available (Morton and Miller, 1973; Morton and Walsby, 1984) but these have concentrated mainly on shores in the North Island and the offshore islands. Although ecological studies on organisms from the Kaikoura region have been published, the only detailed intertidal community work is contained in an unpublished Ph.D. thesis by Rasmussen (1965). In his book on the natural history of Canterbury, Knox (1969) provides detailed zonation patterns present on hard shores around Canterbury and Banks Peninsula.

As a prerequisite for field manipulation experiments, a base-line quantitative survey was undertaken of the intertidal areas around the Kaikoura Peninsula during the summer of 1980 (Marsden, 1981). The aim of the present paper is to investigate community structure and patterns of vertical distribution of intertidal organisms in relation to the physical and biological nature of the habitat. For certain transects, multivariate techniques were used to calculate dissimilarity indices and the usefulness of this technique in detecting pattern is discussed.

SURVEY PROCEDURES AND METHODS

Thirteen survey areas, at approximately 0.8 km intervals around the Kaikoura Peninsula, representative of a range of substratum type, aspect and exposure condition were chosen (Fig. 1). In each area a transect marked by fixed points at upper tidal levels, was surveyed by the Department of Lands and Survey, Blenheim. Eight of the intertidal areas corresponded with those chosen by Rasmussen (1965). Two parallel transects, 1 m apart were marked with a tape from the high water mark down to the extreme low water mark. Samples were collected from sites at 200 mm height intervals down the shore, and on long platforms, samples were collected at 5 m intervals along the tape.

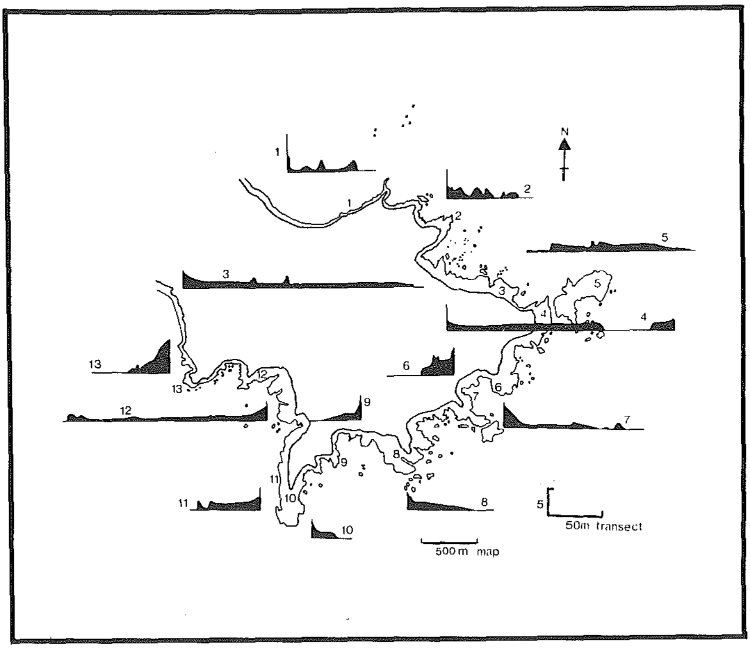

Fig. 1. Kaikoura Peninsula showing survey areas and shore profiles of transects.

Population densities of the larger invertebrates and algae (% cover) were recorded using quadrats, 1/20 m^2 in upper levels and 1/10 m^2 at lower tidal levels. Where boulders or stones were present at a station, they were turned over and examined. Descriptive notes were made of high, mid and low shore levels and a habitat heterogeneity score accumulated by recording the presence of crevices, stones, boulders, channels and algal canopy. The density information from replicate transects were combined and average density plotted against tidal height. The exposure scale devised by Rasmussen (1965), (cited in Jansen 1971) together with local information allowed the survey areas to be ranked in terms of exposure. Further details of these are given in Table 1.

Table 1. Summary of main features of survey areas.

Transect No.	Lgth	D	E	E^1	S	T	U	L	V	N	H^1
1	64	NW	3-4	11	L	P	3.4	0.2	3.2	78	1
2	61	N	3	7	L	I	2.4	-0.2	2.6	64	3
3	214	NE	4	14	S	P	2.4	0.4	2.6	46	13
4	198	E	3-4	10	S	P	2.3	-0.4	3.5	70	5
5a	37	W	1	2	S	P	1.8	0	1.8	39	14
5b	80	E	1	1	S	P	1.0	0	1.0	62	10
6	33	SW	3	8	L	I	3.2	-0.2	3.4	52	7
7	102	SE	4	13	L	P	>3.6	-0.6	8.6	72	5
8	62	S	2-3	5	L	P	1.9	-0.6	3.6	42	7
9	40	SE	3-4	9	L	I	3.4	-0.8	5.3	48	11
10	46	SE	1	3	L/S	I	2.0	-1.4	3.8	79	2
11	54	W	2	4	S	P	2.4	0.6	1.8	67	7
12	163	SW	3-4	12	S	P	1.6	-0.4	3.2	52	7
13	44	SW	3	6	L	I	3.0	0	6.0	49	3

Lgth - length (m)
D - direction
E - exposure scale 1-4 (1 = most exposed)
E^1 - exposure rank (1 = most exposed)
S - substratum: L, limestone; S, siltstone
T - topography: P, platform; I, irregular
U - upper limit
L - lower limit
V - vertical range (m)
N - total species number
H^1 - heterogeneity rank (1 = most heterogenous)

Four transects (1, 6, 9, 13) in which there was rocky substratum throughout the intertidal range, were used for community analysis using the Canberra metric dissimilarity measure. This was analysed using an updated programme of Taxon 2 generated by the C.S.I.R.O. laboratory based at the University of Queensland, Brisbane. This similarity index is regarded as being sensitive to common species and has been used successfully to define major faunal assemblages amongst the mollusc fauna of Western Port, Victoria, Australia (Coleman and Cuff, 1980), and subtidal benthos off the Otago Peninsula, New Zealand (Probert and Wilson, 1984).

STUDY AREA

The Kaikoura Peninsula is a hilly plateau projecting out from the Marlborough Coast. The land slopes steeply to the sea mainly towards the north-east, south-west and south-east, forming a narrow platform which then slopes rapidly from the intertidal area to the sea floor. Along the northeast and south-west faces of the Peninsula, limestone and siltstone platforms alternate. Characteristically, the limestone surfaces are rough and markedly folded in contrast with the mudstone or siltstone platforms which are broad and smooth. The winds are predominantly from the south and south-west in the winter, and from the north-east in the summer (Rasmussen, 1965). The salinity varies between 33.5 and 35 ppt through the year with highest values recorded during the summer (Records kindly supplied by N.Z. Oceanographic Institute, D.S.I.R.). There are no rivers or sizeable streams entering the intertidal regions.

Despite its small size the Peninsula has an extensive intertidal area, 14 km long with platforms extending seawards for more than 100 m. The rocky shores are typically irregular in profile and zonation patterns are not obvious except in certain locations with gently or steeply sloping platforms.

DISTRIBUTION OF ORGANISMS

Fig. 2 shows the distribution of dominant macroinvertebrates and algae on a moderately sheltered shore just below the Edward Percival Field Station. On this transect, a total of 78 species were recorded, with the invertebrates dominated by littorinids and other grazing molluscs. The densities of the dominant organisms plotted against tidal height are shown as kite diagrams

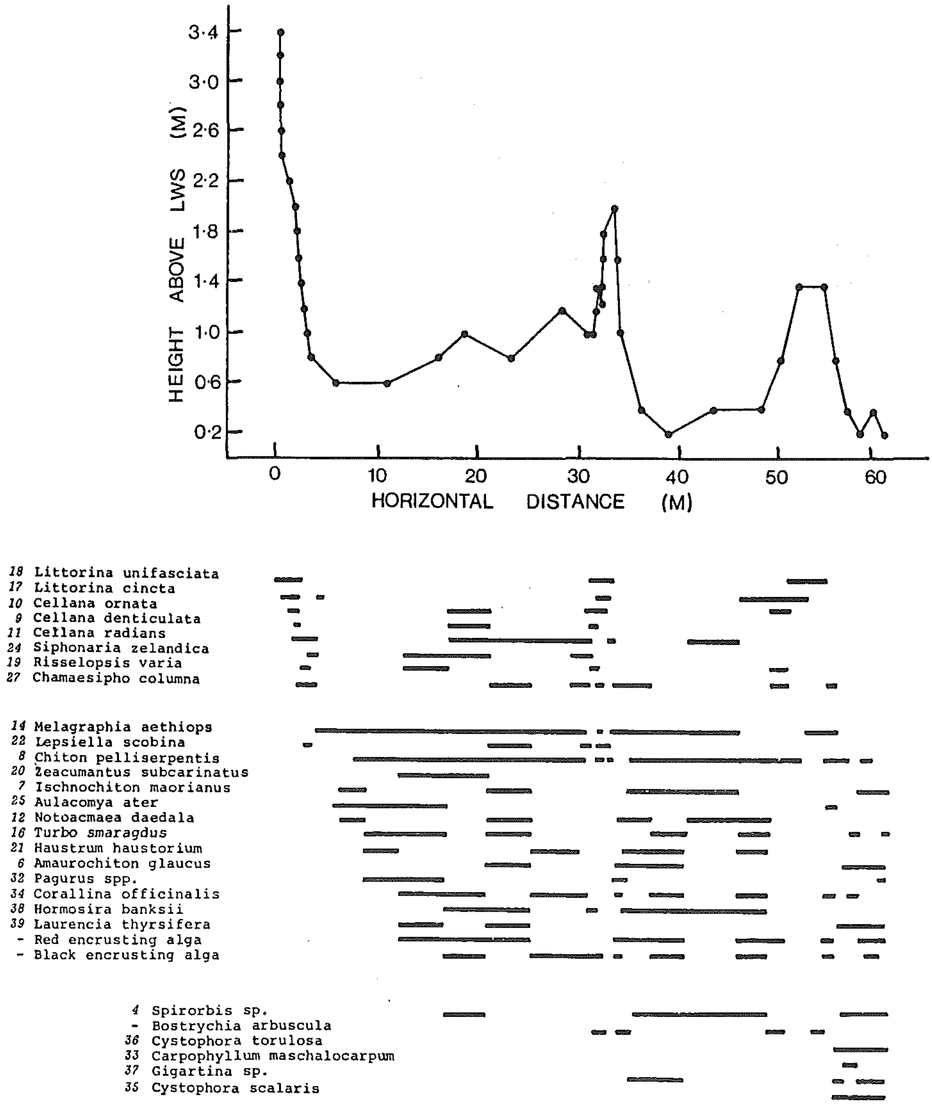

Fig. 2. Transect 1, laboratory rocks showing major species distribution in relation to tidal height and distance down the shore. The numbers alongside the species are those used in the pattern analyses.

in Fig. 3 for those species found in more than 25% of the samples. These include the small banded periwinkle *Littorina unifasciata* found at highest tidal levels with *Littorina cincta* and the

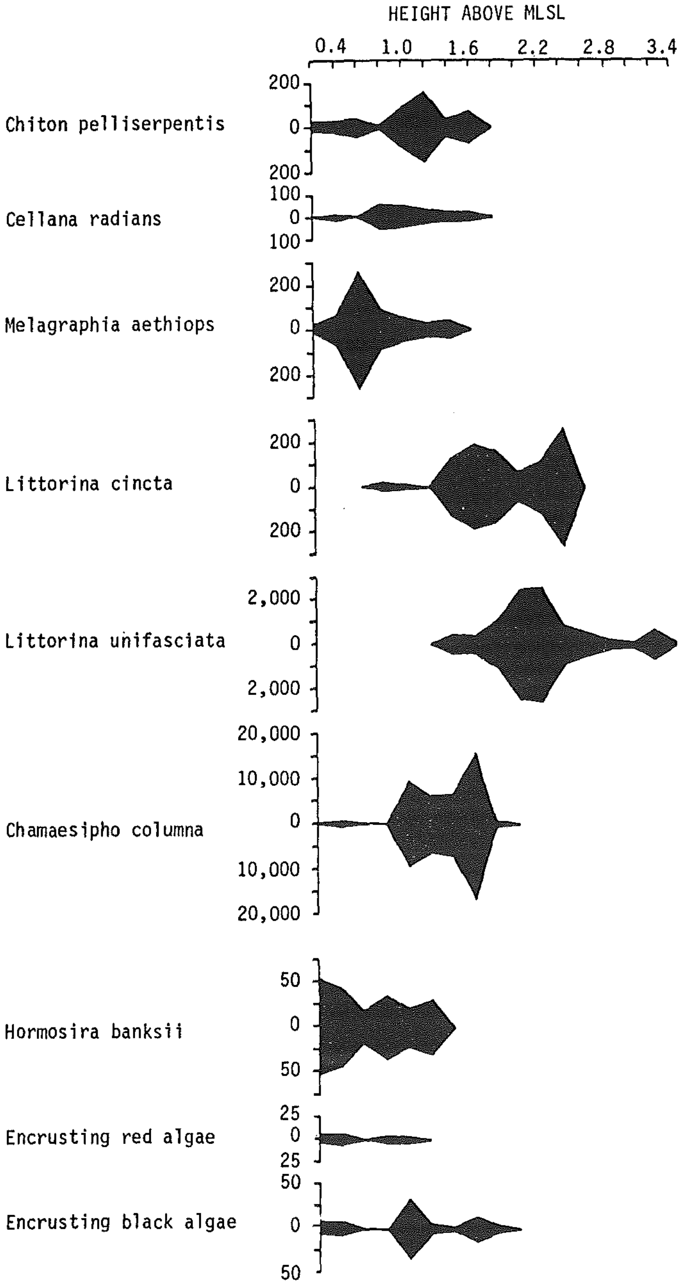

Fig. 3. Kite diagrams showing the density/m^2 of dominant organisms from transect 1 plotted against tidal height.

barnacle *Chamaesipho columna* below. The typical mid tide grazers included *Chiton (Sypharochiton) pelliserpentis, Cellana radians* and *Melagraphia aethiops.* At lower tidal levels the characteristic brown algae were *Hormosira banksii, Cystophora* spp. and *Carpophyllum maschalocarpum.*

Kite diagrams were drawn for all 13 transects relating the density of macroinvertebrates and algae with tidal height (Marsden, 1981). The sites were ranked according to their level of exposure to wave action and species lists compared noting the presence or absence of dominant groups and their tidal range. This information was used to construct a diagramatic representation (Fig. 4) showing the changes in zonation pattern of dominant

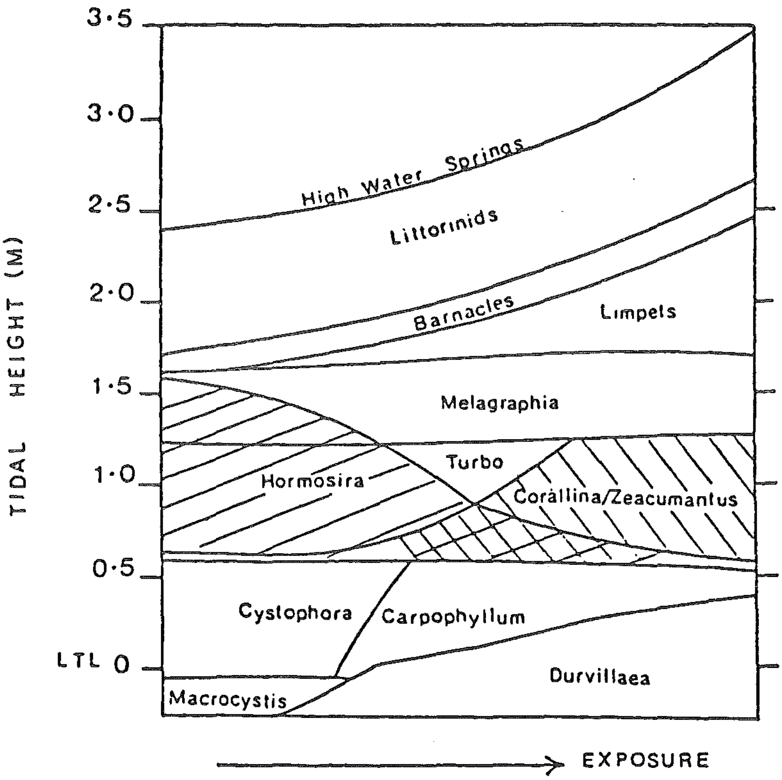

Fig. 4. Diagramatic representation describing the effect of exposure to wave action on the distribution of indicator species around the Kaikoura Peninsula.

plants and animals of the Kaikoura Peninsula with increased exposure. This shows the upshore displacement of species such as the littorinids and *Durvillaea*. Also, coralline algae, *Carpophyllum maschalocarpum* and *Durvillaea* typically replaced *Cystophora* and *Macrocystis* under extreme exposure. These patterns are consistent with those described for Banks Peninsula, Canterbury (Knox, 1969).

ABUNDANCE AND OPTIMAL SHORE LEVEL FOR DOMINANT MACROINVERTEBRATES AND ALGAE

The total species list recorded in the survey includes 123 species of macroinvertebrates and fishes and 45 species of algae. Of the 47 common species (Table 2), 8 species were identified as being characteristic of these southern shores. They were the littorinids *L. unifasciata* and *L. cincta*, the top shells, *Melagraphia aethiops* and *Turbo smaragdus* and the limpet, *Cellana denticulata*. The exposed shore barnacle *Epopella plicata* and two species of algae, *Hormosira banksii* and *Carpophyllum maschalocarpum* completed the list. The average abundance of these species in quadrats where they occurred are shown in Table 2; Figs 5 and 6 show the tidal range and level of maximal density for each species plotted for each transect ranked according to its degree of exposure to wave action.

The distribution of the upper shore littorinid *L. unifasciata* was considered to depend upon both the degree of exposure to wave action and the availability of suitable upper shore substrate. This latter feature appears to be a limiting factor on the most exposed parts of the Peninsula such as Seal Reef (Sites 4 and 5), parts of which rise only 1.5 m above the low water mark. The average density of *L. unifasciata* was 508.8/m^2 (SE = ± 199.9) but higher values were obtained on shores of intermediate exposure and where the vertical range was not truncated. The height at which maximum density occurred varied considerably between transects ($\bar{x}$ = 1.78 m above low water; SE = 0.18) but showed no direct relationship with either exposure level or substratum availability. *Littorina unifasciata* was more abundant than *L. cincta* which had an average density/m^2 of 198.8 (SE ± 54.8). Highest densities of *L. cincta* were recorded at an average tidal height, 1.72 m above sea level (SE = ± 0.12) which was similar to the optimal height for *L. unifasciata*. The lower limit of *L. cincta*, however, extended markedly downshore on some transects. The density of *L. cincta*, as with the density of *L. unifasciata* did not correlate with any of the shore variables measured. A comparison of the densities of the two littorinid species within individual quadrats suggested that the density of *L. cincta* was not directly related to the numbers of

Table 2. Density $/m^2$ of main species and invertebrate feeding groups herbivores (H), omnivores (O) and carnivores (C). The numbers refer to those used in pattern analyses

Species No.		Feeding group	1	2	3	4	5a	5b	6	7	8	9	10	11	12	13
1	*Anthopleura* sp.	C	15	27	70	160	5	5	30	28	10	30	38	163	10	38
2	*Cricophorus nutrix*	C	0	60	10	40	0	0	35	48	0	40	10	120	0	10
3	*Isactinia olivacea*	C	10	10	10	0	0	0	38	22	16	0	0	10	27	21
	Perinereis novaehollandiae	C	0	10	0	0	0	10	0	0	10	18	10	35	13	0
4	*Spirorbis* sp. (x 10^2)	F	24	20	4	23	31	7	17	20	19	2	5	23	16	6
6	*Amaurochiton glaucus*	H	30	23	10	10	20	0	20	30	13	0	20	0	13	20
7	*Ischnochiton maorianus*	H	36	27	20	0	5	33	117	35	61	0	53	85	40	90
8	*Chiton pelliserpentis*	H	53	55	31	70	23	11	48	14	8	10	10	17	14	27
9	*Cellana denticulata*	H	42	69	20	90	23	15	41	14	13	43	45	43	0	50
10	*Cellana ornata*	H	45	33	60	34	10	18	10	15	5	46	90	23	0	20
11	*Cellana radians*	H	36	0	0	26	0	0	15	13	0	0	13	10	0	10
	Notoacmea daedala	H	52	75	40	6	20	5	20	20	8	0	10	0	0	0
13	*Patelloidea corticata*	H	10	10	0	23	23	20	0	5	0	0	10	50	5	24
	Cantharidella tesselata	H	20	10	10	10	0	5	0	5	0	0	75	0	0	0
	Herpetopoma bella	H	0	0	0	0	0	20	20	10	0	0	10	20	5	10
14	*Melagraphia aethiops*	H	83	54	55	121	41	19	54	61	47	0	70	47	48	54
16	*Turbo smaragdus*	H	39	108	86	46	14	66	108	17	5	10	32	30	16	30
17	*Littorina cincta*	H	136	482	186	195	0	15	584	0	21	49	499	334	15	267
18	*Littorina unifasciata* (x 10)	H	84	214	61	30	2	0.5	270	0	13	60	20	44	14	73
19	*Risellopsis varia*	H	62	86	17	13	20	32	18	15	500	206	25	33	15	0
	Estea sp.	H	100	27	0	0	0	5	30	23	175	0	20	0	0	150
20	*Zeacumantus subcarinatus* (x 10)	H	14	62	105	51	105	41	14	11	143	0	33	189	45	31
21	*Haustrum haustorium*	P	24	18	13	10	10	10	10	7	8	0	0	10	0	10
22	*Lepsiella scobina scobina*	P	32	25	20	0	0	0	0	13	0	20	10	35	0	20
	Cominella maculosa	P	10	30	15	40	13	10	0	8	18	0	25	0	22	0
24	*Siphonaria zelandica*	H	20	18	10	65	10	21	10	9	5	28	15	51	13	15
25	*Aulacomya ater*	S	73	70	0	0	71	120	65	18	0	30	60	200	0	93
28	*Chamaesipho brunnea* (x 10^2)	S	0	0	4	43	8	2	0	0	0	37	22	19	0	0
27	*Chamaesipho columna* (x 10^2)	S	80	51	118	16	0	0	0.5	8	0	23	8	8	0	0
29	*Epopella plicata*	S	0	80	93	43	17	61	10	0	0	101	20	193	0	0
30	*Exosphaeroma obtusum*	O	20	0	0	25	0	0	100	0	5	10	20	10	0	0
32	*Pagurus* spp.	O	24	0	40	0	0	5	90	10	0	0	20	40	8	50
	Petrolisthes elongatus	S	10	0	0	0	5	0	10	18	5	0	20	0	15	150
	Tripterygia varium		18	10	10	0	0	0	0	20	5	0	10	0	25	30
	Enteromorpha sp.		30	0	1	26	0	15	0	0	17	0	3	2	1	0
40	*Ulva* sp.		0	0	0	0	0	0	0	2	6	38	7	1	1	6
33	*Carpophyllum maschalocarpum*		6	20	40	25	30	25	25	0	0	10	10	0	0	0
	Colpomenia sinuosa		5	2	4	4	1	2	0	2	1	13	8	4	5	0
35	*Cystophora scalaris*		1	3	0	8	10	15	8	10	0	25	11	21	11	16
36	*Cystophora torulosa*		1	15	15	24	0	0	3	43	5	3	0	0	6	3
	Glossophora kunthii		0	0	0	14	0	10	5	1	0	25	19	3	3	0
	Halopteris paniculata		0	29	3	16	0	5	0	5	0	3	6	5	0	3
38	*Hormosira banksii*		37	28	34	39	0	5	25	29	3	10	1	8	21	13
	Macrocystis pyrifera		0	25	0	10	0	1	38	0	0	38	33	3	0	0
34	*Corallina officinalis*		18	34	40	30	19	18	10	17	4	24	11	21	11	16
	Laurencia thyrsifera		4	25	0	15	5	5	6	5	0	5	4	0	0	5
	Encrusting black alga		13	0	4	7	2	3	10	18	13	0	17	17	2	5
	Encrusting red alga		4	15	17	23	28	19	42	18	14	5	18	8	11	3

L. unifasciata present.

The limpet *Cellana denticulata* was found on all shores examined on the Kaikoura Peninsula except Mudstone Bay (transect 12). Greatest densities were found on shores of intermediate wave action but the largest individuals were recorded from the most exposed sites. In general, barnacles were not a conspicuous element of the fauna on the Peninsula, probably due to the fragmentary nature of the limestone and the difficulty of

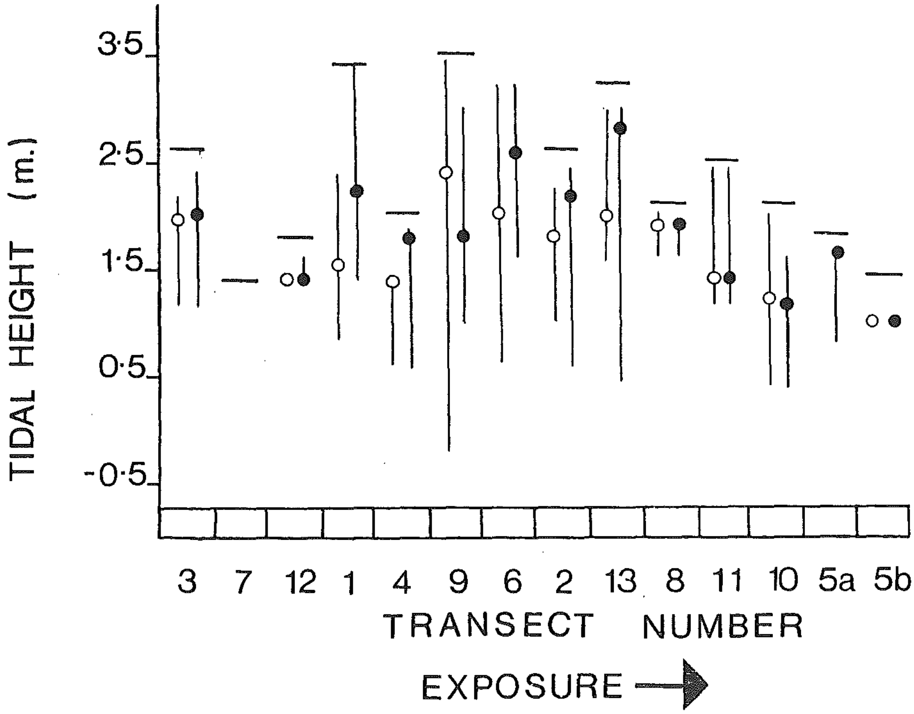

Fig. 5. Vertical range and level of greatest density of dominant macro-invertebrates and algae plotted against transects, ranked according to exposure level: A, *Cellana denticulata* (open circles), *Epopella plicata* (closed circles); B, *Melagraphia aethiops* (open circles), *Turbo smaragdus* (closed circles); C, *Hormosira banksii* (open circles), *Carpophyllum maschalocarpum* (closed circles).

adhesion on the soft mudstone. Three species were found at shore levels below the littorinids, *Chamaesipho columna*, *C. brunnea* and *Epopella plicata*. The latter barnacle was absent from the most sheltered locations but formed a dominant band on exposed shores often on the lee side of ridges. Its distribution coincided with the limpet *C. denticulata*.

The top shell *Melagraphia aethiops* was the dominant mid shore grazer at Kaikoura. Its distribution changed little with wave exposure and average densities greater than $50/m^2$ were recorded on all but the most exposed platforms. The vertical range of this species extended from 0.5 to 2 m above the low water mark. The catseye *Turbo smaragdus* was often found at

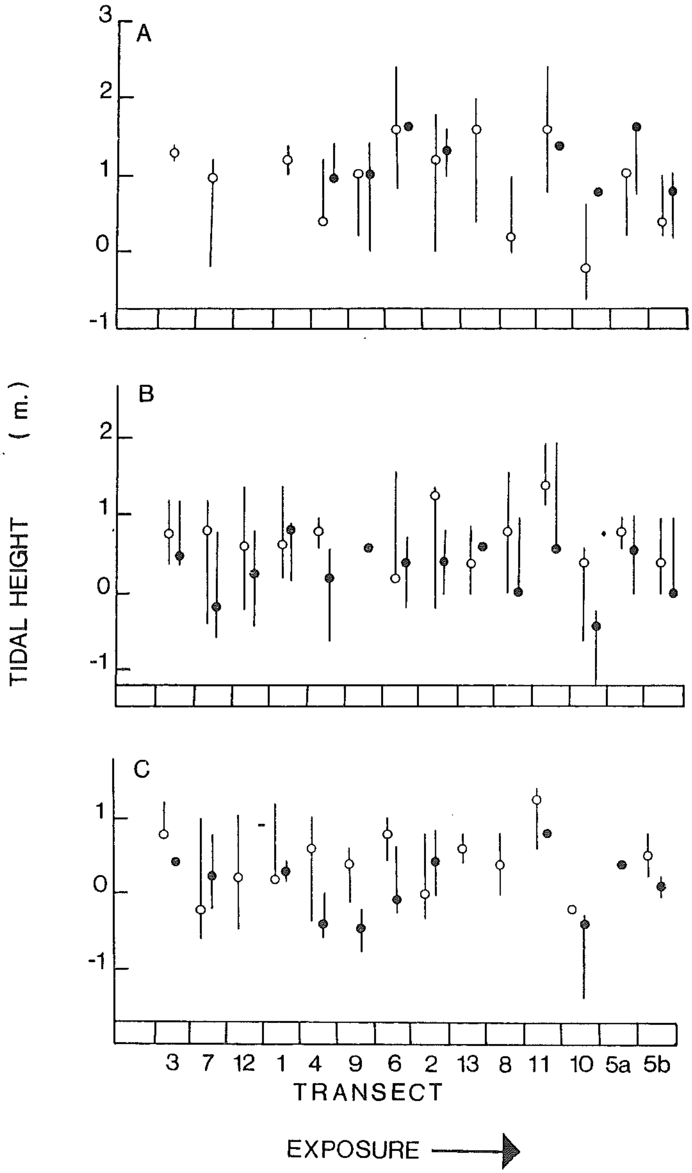

Fig. 6. Vertical range and level of greatest density of dominant macro-invertebrates and algae plotted against transects, ranked according to exposure level: A, *Cellana denticulata* (open circles), *Epopella plicata* (closed circles; B, *Melagraphia aethiops* (open circles, *Turbo smaragdus* (closed circles); C, *Hormosira banksii* (open circles), *Carpophyllum maschalocarpum* (closed circles).

similar tidal levels to *Melagraphia* but generally extended into lower tide levels. While very high densities of *Turbo* were recorded on sheltered and moderately exposed shores around the Peninsula, large individuals were found below boulders on even the most exposed shores.

The necklace weed *Hormosira banksii* was the characteristic mid littoral fucoid. It was found in sheltered locations on most shores including the exposed reef (T5). *Hormosira* formed a wide band on gently sloping sheltered platforms and extended from 1.4 m above the low water mark to -0.4 m below it. *Carpophyllum maschalocarpum* formed a conspicuous belt at lower tide levels than *Hormosira* and was the dominant lower shore alga on sheltered shores. On rocky promontories of intermediate wave action, *Carpophyllum* extended further up the shore and this species was also common in intertidal rock pools and channels. On the most exposed or steeply sloping intertidal shores *Carpophyllum* was commonly replaced by the bull kelp *Durvillaea* spp.

PATTERN ANALYSES

Four transects, one of irregular topography (1) and three with more regularly sloping profiles (6, 9, 13) were used for the multivariate analyses aimed at detecting underlying patterns within the community. These transects were the only ones in which organisms were not limited by a lack of rocky substrata at upper shore levels. Dendrograms (both normal and inverse classifications) were prepared, initially by considering the invertebrates alone, and later by including the algae. In the survey the algae were recorded as % cover rather than by the number of individuals; however this did not affect the overall groupings of the invertebrates. For the overall analyses, 40 animal and plant species common to the four transects were used. These are numbered in Table 2 and in the legend to Fig. 7.

Analyses of the data collected from transect 1 and illustrated earlier (Fig. 2) suggested a pattern involving either 3 or 7 groups of species. All 7 groups contained algae and invertebrate representatives of all shore levels and feeding types (Fig. 7a). The main factors responsible for the variation and classification into the species groups (A) or (B) were the densities of five species, *Littorina unifasciata*, *L. cincta*, *Melagraphia aethiops*, *Chiton (Sypharochiton) pelliserpentis* and *Hormosira banksii*. The average height of samples included in (A) was 2.27 m and this was made up of 2 subgroups (dissimilarity > 1.5) with heights of 3.0 and 1.86 m above low water. Species group (B) corresponded to samples on average 0.86 m above low water, but further subgroups did not correlate with tidal heights.

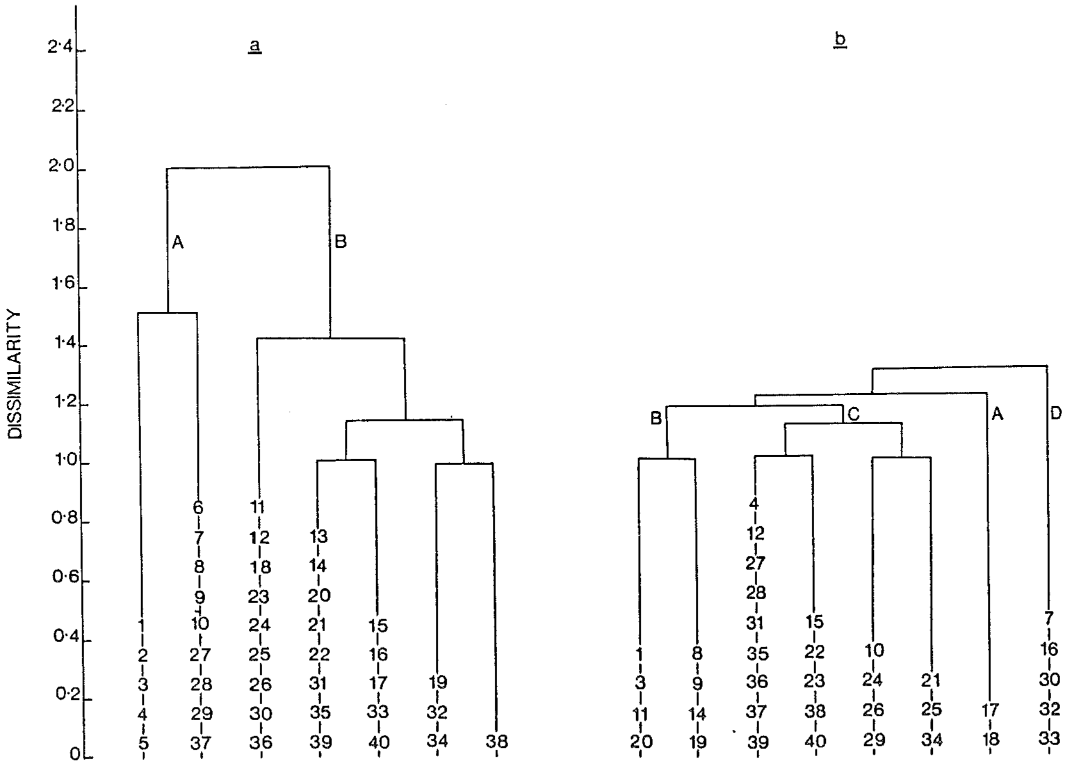

Fig. 7. Dendrograms showing cluster analysis between species in transect 1 (a) and transects 6 and 9 combined (b). The numbers refer to individual species, most of which are listed in Table 2. These include: *Acanthochitona zelandica* (5), *Notoacmea parviconoidae* (12), *Micrelenchus dilatatus* (15), *Xymene* sp. (23), *Mytilus edulis aoteanus* (26), *Ligia novaezealandiae* (31), *Gigartina* spp. (37), *Laurentia thyrsifera* (39).

In contrast with these results, the combined data from transects 6 and 9 detected a pattern (Fig. 7b) which corresponded to a biological separation of the groups. The classification identified four major species groups, a high shore group (A) consisting of the two littorinid species, a mid shore assemblage of grazing molluscs and anemones (B), a sessile invertebrate group, which also contained algae (C) and a low shore group (D) including *Turbo smaragdus* and *Carpophyllum maschalocarpum*.

The classification of the 58 quadrat samples included in transects 6 and 9 are shown in Fig. 8. The dendrogram illustrates that samples from the same transect and location were the most similar. At the 12 group level, (which may not be the correct level to look at for distinguishing pattern), four groups exclusively contain samples from transect 9 and three exclusively

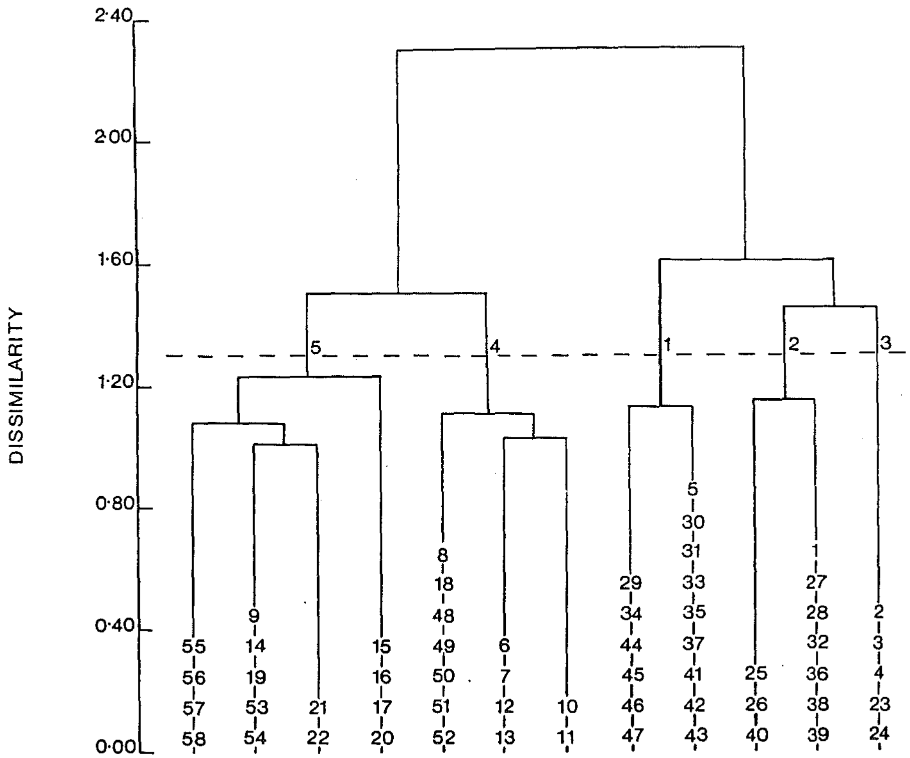

Fig. 8. Dendrogram showing cluster analyses of combined sites from transect 6 (samples 1 - 22) and 9 (samples 23 - 58).

from transect 6. Only three groups contain samples from both transects. The combined samples from transects 6 and 9 were classified into 5 groups with dissimilarity indices above 1.4. The main sources of variation giving rise to the pattern were the densities of the limpet *Cellana denticulata* and the two species of littorinids. However, these accounted for only 14% of the total variation. Group 1 was dominated by samples of average height 2.72 m (SE = ± 0.09) above low water in which the density of *L. unifasciata* was high. This contrasted with group 2 in which *Littorina cincta* was either absent or occurred at a similar density to *L. unifasciata* (height 2.6 m, SE = ± 0.16 above low water). Group 3 was generally of mid-tide levels from transect 6 (height 2.09, SE = ± 0.22) in which the density of *L. unifasciata* was low and *L. cincta* was high. Mid-tide organisms from transect 9 ($\bar{x}$ height 0.95, SE = ± 0.12) were the major source of variation in group 4 which included *Epopella plicata, Chamaesipho columna, Chiton pelliserpentis* and *Cellana denticulata*. These last 2 species were absent from group 5 where the samples were dominated by *Hormosira, Corallina* and *Carpophyllum*. This group consisted of low shore samples from both transects ($\bar{x}$ height = 0.2 m below low water, SE = ± 0.13).

To provide an indication of the general pattern on shores around the Kaikoura Peninsula 113 samples (sites) from transects 1, 6, 9 and 13 were combined and analysed using principal coordinates ordination (PCOORD). Fig. 9 illustrates the minimum spanning tree of the sites from the four transects showing the first order relationships with their closest neighbours. There were 32 sites in which the second closest neighbour was within 0.02 of the first closest neighbour. Consideration of these, however, did not alter the tree greatly as they tended to strengthen the obvious similarities between adjacent sites. The results show a high degree of similarity between samples both

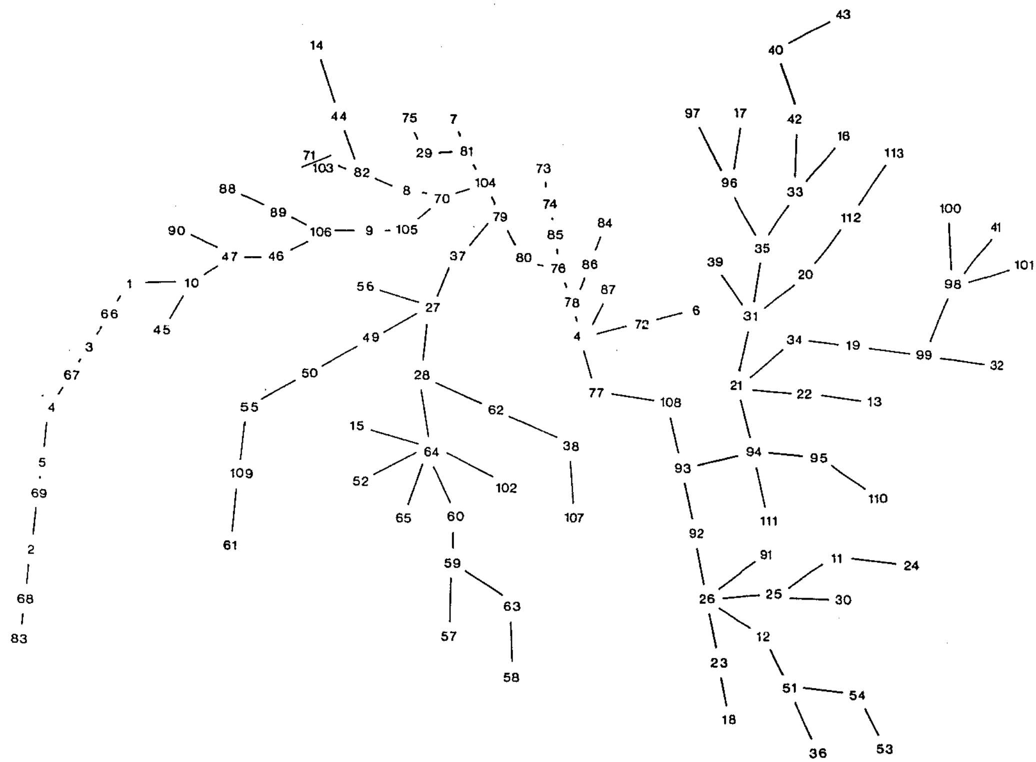

Fig. 9. Minimum spanning tree showing the first closest neighbours of sites from transect 1(1 - 43), transect 6 (44 - 79), transect 9 (80 - 101) and transect 13 (102 - 113). The length of the bar is a measure of the degree of similarity.

within and between transects. Also there were no major branches of the minimum spanning tree consisting of sites from only one transect. The classification identified 5 groups of sites (Fig. 10). Group 1 sites contained samples dominated by four mollusc species which accounted for 64.6% of the variation. These were *Cellana denticulata*, *Notoacmea parviconoidea*, *Melagraphia aethiops* and *Risselopsis varia*. The sites included in the group occurred an average distance of 1.45 m along the transect from the high water mark. While groups 2 and 3 contained similar species to group 1, they corresponded with transect number and sample rather than any distance or tidal height information. Group 3 had a subgroup 3A, where samples were located an average distance of 4.6 m from the high water mark. Here the density of *L. cincta* accounted for 84% of the variation. The residual sites in group 3 were found further down the shore, an average distance of 13.5 m from the high tide mark. Group 4 included sites characteristic of

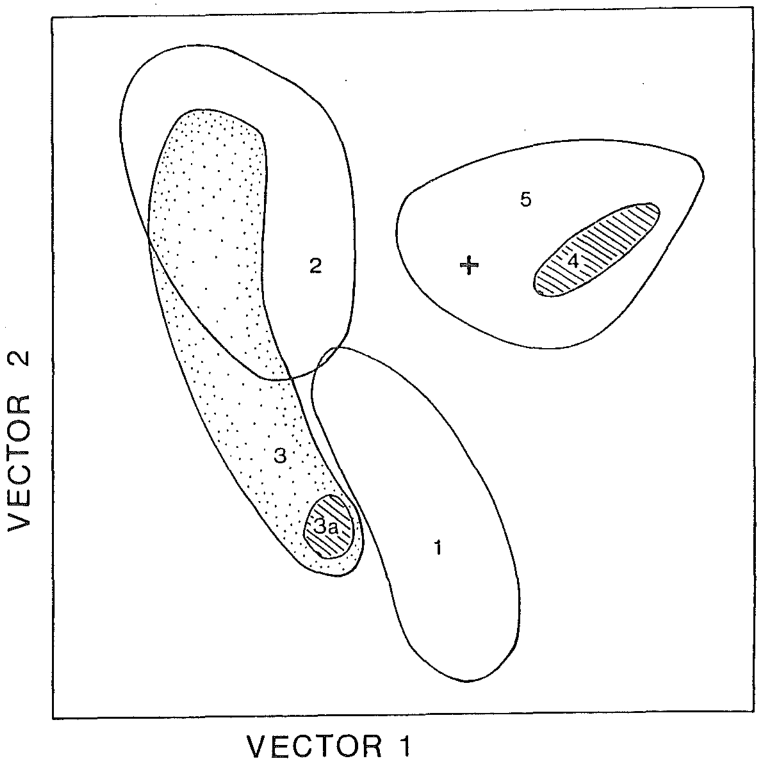

Fig. 10. Principal coordinates (PCOORD) ordination results for the combined sites from transects 1, 6, 9 and 13 showing the relationships of the 5 site groups.

mid-shore samples of average height above low water of 1.19 m. Within this group there were considerable variations in the densities of the algae *Ulva* and *Gigartina*. The final group (5) corresponded to an average height above low water of 0.55 m, and was separated from group 4 mainly due to *Cellana ornata* and *Chamaesipho brunnea* which were present in group 4 but not in group 5. Fig. 10 shows the PCOORD results from the classification which illustrates the closeness of the five groups. Only one important direction was evident with an Eigen value of 5.88. However, this vector accounted for only 11.64% of the variation. The direction of this vector was strongly correlated with the densities of *L. unifasciata*, *L. cincta*, *M. aethiops*, *C. denticulata* and *C. columna*. Both height and to a lesser extent distance were positively correlated with the direction of the vector.

FUNCTIONAL GROUPS

The numbers of species of macrofauna and flora recorded per transect on the Kaikoura Peninsula ranged between 39 species for transect 5a, to 79 species on transect 10 (Table 3). Invertebrates were abundant at all transect sites and molluscs, mainly gastropods, were the dominant group (Table 2). Most functional feeding types, herbivores, suspension feeders, and carnivores were represented. Deposit feeders however were not amongst the dominant groups. For the algae, crustose coralline algae were found on all transects and the low shore of all transects contained a diverse range of delicate red algae as well as the larger more conspicuous blade-like brown algae.

For each transect, the average density of each functional feeding group or algal type was calculated and plotted against exposure rank and heterogeneity of the transect. These results indicated that exposure level had little effect on the density of any of the animal or plant groups but there was some indication that heterogeneity might be important (Fig. 11). Apart from transect 4 in which there was an unusually high density of filter feeders, the density of this group generally increased in the more heterogenous habitats. The density of grazers appeared high on all shores and predators appeared greatest on the shores of intermediate values.

The relationship between the density or organisms in the functional groups and substratum type is shown in Table 4, with details of the topography of the transect shown in Table 2. The overall density of grazers was similar on all shore types, filter feeders were more abundant on shores of mixed substratum types, and predators and omnivores appeared in greater densities on shores predominantly of limestone where there would be more

Table 3 Number of species belonging to major taxonomic groups of the Kaikoura Peninsula survey.

	T1	T2	T3	T4	T5a	T5b	T6	T7	T8	T9	T10	T11	T12	T13
Sea anemones	4	4	3	2	4	4	3	5	3	2	3	6	4	3
Polychaetes	5	4	1	–	1	2	2	3	4	2	4	3	4	1
Mollusca (Total)	38	32	22	32	21	31	23	34	21	16	33	26	23	24
Whelks	5	3	4	3	2	2	1	5	2	2	3	2	4	3
Gastropods	7	10	8	9	4	11	11	9	8	5	6	10	8	6
Chitons	5	4	3	3	4	3	3	5	4	1	3	2	5	4
Limpets	9	8	4	9	6	7	5	7	3	3	8	5	1	6
Trochids	4	4	2	5	2	3	3	5	3	1	5	2	3	3
Bivalves	3	3	1	3	3	5	–	3	1	4	3	5	2	2
Crustacea	10	6	7	12	8	10	12	6	5	10	14	11	6	7
Echinoderms	–	1	2	1	–	–	–	–	–	–	2	2	–	–
Total algae	17	16	10	19	10	16	11	18	8	18	20	18	12	13
Total species	78	64	46	70	39	62	52	72	42	48	79	67	52	49

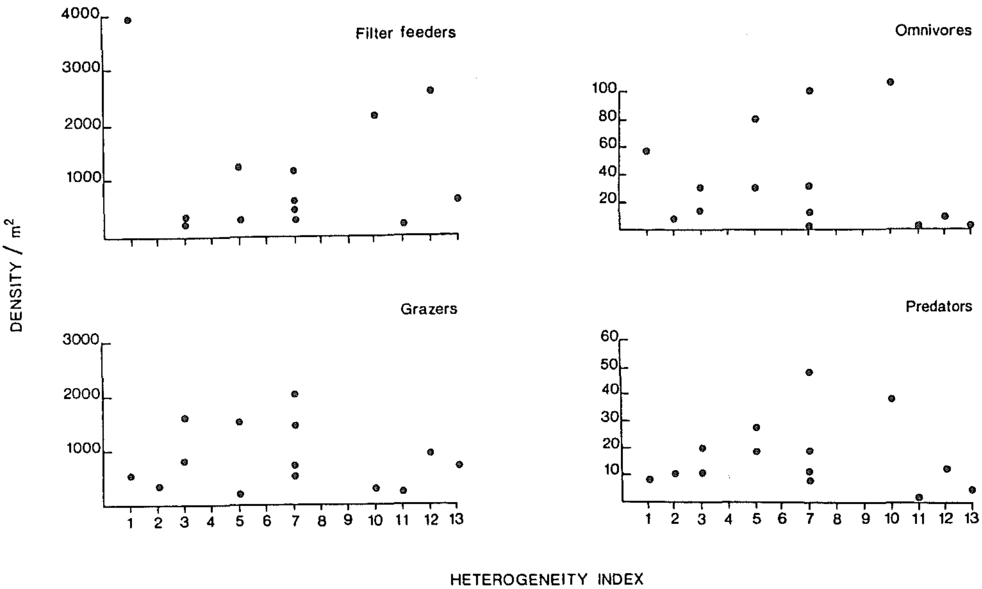

Fig. 11. Relationship between the average density of invertebrate feeding types and habitat heterogeneity for filter feeders (A), grazers (B), omnivores (C) and predators (D).

available crevices.

Using the number of species present as an index of species diversity, there was no correlation (Spearman Rank Correlation coefficient rs $P > 0.5$) between the number of algae or total species and exposure rank, length or the upper or lower tidal height of the transect. While substratum type, either limestone or mudstone, may have excluded certain species, the total number of species present within the two substrate types was similar (limestone $\bar{x} = 58.8$, SE = $\pm$ 6.0); mudstone $\bar{x} = 52$, SE = $\pm$ 4.7. A close correlation was found between the number of species of algae and invertebrates present on any transect (rs = 0.62, $P = 0.05$, df = 12). The total number of species was correlated with habitat heterogeneity (rs = 0.70, $P = 0.1$, df = 12) such that shores with complex topography at all shore levels had the most diverse fauna and flora. Habitat heterogeneity was not strictly related to exposure and the most biologically diverse habitats were those of moderate rather than strongly exposed aspect. Species diversity in all transects increased seawards along with the availability of specialised and sheltered microhabitats.

Table 4 Density of functional groups in relation to substratum type.

	Mudstone	Limestone	Mixed
Invertebrates ($\bar{x}$ /m^2 ± SE)	(3,4,5a,5b,11,12)	(2,7,8,9,13)	(1,6,10)
Filter feeders	1028 ± 367	803 ± 373	1770 ± 1186
Grazers	803 ± 186	1001 ± 301	986 ± 546
Predators	15 ± 7.1	24 ± 10.1	9 ± 0.5
Omnivores	35 ± 15.6	83 ± 19.5	29 ± 15.5
Algae (% cover ± SE)			
Small	3 ± 0.9	8 ± 1.8	8 ± 7.6
Crustose	13 ± 1.82	10 ± 3.6	10 ± 2.1
Blade	9 ± 2.0	14 ± 5.5	9 ± 2.3
Divided	7 ± 2.0	5 ± 3.5	2 ± 0.9

DISCUSSION

Shores around the Kaikoura Peninsula have a diverse fauna and flora with an average of 58.6 species (SE = ± 3.7) found at any locality. This was high in comparison with similar surveys carried out along the Canterbury (Knox, 1953) and Marlborough coastline (Marsden and Fenwick, 1978). The fauna was dominated by gastropods, and population densities of the common invertebrates varied considerably both within and between survey areas. Eight common species were used as indicator species; *Littorina unifasciata*, *Littorina cincta*, the limpet *Cellana denticulata*, the barnacle *Epopella plicata*, two topshells - *Melagraphia aethiops* and *Turbo smaragdus*, and two algae *Hormosira banksii* and *Carpophyllum maschalocarpum*. For most of these species, an optimal level where density was maximal could be found but this was not greatly affected by degree of exposure to wave action.

The vertical distribution of organisms on the Kaikoura shores can be compared with those on Taylors Mistake and Banks Peninsula (Knox 1953, Knox 1969). The irregular platforms characteristic of the Kaikoura Peninsula have a reduced barnacle cover and increase densities of grazing animals such as limpets and pulmonate limpets. Several species of a typically northern distribution (Knox, 1969) occur at Kaikoura. These included the barnacle *C. brunnea*, the limpets *C. denticulata* and *C. flava* and the crab *Heterozius rotundifrons*. There were also southern species, the limpet *C. strigilis* and algae such as *Durvillaea antarctica*, *Macrocystis pyrifera*, *Halopteris congesta* and *Desmarestia firma*. The upper tidal levels on Canterbury and Marlborough shores were characterised by the presence of the two littorinids, *L. unifasciata* and *L. cincta*. The former species is regarded as being more northern in distribution and is also found in Western Australia and New South Wales. In contrast to Taylors Mistake, the upper vertical limit of *L. cincta* in the Kaikoura region, was below that of *L. unifasciata*, a feature also recorded for North Island shores (Morton and Miller, 1967). Some species found at Kaikoura are common to New Zealand and Australia. For these species, which included *Hormosira banksii*, *Corallina officinalis* and *Ulva lactuca* the distribution patterns conform to the general patterns described in Morton and Miller (1967) and Underwood (1981).

The translation of the transect data according to tidal height revealed characteristic sequences of organisms on the shore rather than distinct bands containing specific species. This supports data collected on British shores by Underwood (1979) on uniformly sloping shores. By visual and quantitative assessments it was possible to divide the shores around Kaikoura into only three major zones corresponding to tidal height. These were the upper littorinid belt, the lower algal zone and an intermediate region dominated by intertidal grazers. The upward distribution of the littorinid belt was limited on the most exposed shores due to the unavailability of suitable substratum.

Dissimilarity coefficients calculated for the species and stations for one moderately sheltered undulating shore below the Marine Laboratory produced three species groupings apparently without any biological significance. In recent years there have been a number of studies which have questioned the use of dissimilarity indices for biological work. Bloom (1981) for example considers that the Canberra metric, by underestimating high values for common species and overestimating low values will tend to obscure cluster relationships. Using such a similarity measure, however, the combined results from transects 6 and 9 identified four distinct groups of species which corresponded to the shore levels previously identified and functional feeding types. Several explanations might be put forward regarding why groupings were apparently not seen following analyses of transect 1. These include the more irregular nature of the habitat, the sample size and the diversity of organisms within each sample. The classification of species in the combined data from transects 6 and 9 separated the mid-tide organisms into the more sessile invertebrates and the algae and the more mobile grazers such as topshells and limpets. Species however did not fall into the 9 zones on the shore according to tidal height as predicted by Stephenson and Stephenson (1949) and also did not divide according to typically northern or southern species associations as found in Seapy and Littler (1980) in California. The functional groups of species distinguished by the analyses of the Kaikoura samples can now be used in generating hypotheses and field experimentation aimed at understanding species group interactions.

Field *et al.* (1982) outlined a practical strategy for analysing multi-species distribution patterns using, as an example, the nematode species from a British estuary. They stress the importance of relating environmental variables to both species and station groups. From the site analyses of samples from four locations around the Peninsula it was shown that sites from the same location were more similar than those between locations. The areas chosen for the analyses represent different levels of exposure and aspect (i.e. probable temperature regime), features which have recently been shown to affect site groupings along the South African coast (McQuaid and Branch, 1984). On the continental shelf off the Otago Peninsula, New Zealand, physical characteristics of the habitat such as depth and sediment have also successfully led to the separation of sites into community types (Probert and Wilson, 1984). In the Kaikoura survey the sites were separated mainly according to height above low water and in some instances distances along the transect. The main species responsible for the variation, resulting in the classification of sites into 5 groups were the two littorinids, *L. cincta* and *L. unifasciata, Melagraphia aethiops, Cellana denticulata and Chamaesipho columna.* Of these, only the latter species had not previously been regarded as important indicator species.

Invertebrates of the Kaikoura intertidal consisted of all feeding types and although the topography and high exposure of intertidal platforms may limit certain species, limestone areas had a similar number of species to mudstone platforms. The major factor which appeared to influence the number of species present was the heterogeneity of the habitat. The species diversity increased seawards with the addition of extra microhabitats associated with crevices, boulders and an algal canopy. With undulating topography or large boulders, shores with very high exposure to wave action also contained some species more characteristic of sheltered conditions.

The present survey attempted to assess the within-site and between-site variation in intertidal organisms and the baseline data generated will be used to monitor changes with time. The programme was not designed to produce a detailed statistical description or analyses of the community, but to identify the species which are important in describing the shores. Such background information will be useful for future studies aimed at understanding how the basic framework of the intertidal habitat is modified by the biotic and physical environment.

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